On Whorled Phyllotaxis.

I

Growth Whorls

By

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1. Introduction. Besides my „Beiträge zur Blattstellungslehre" which appear in this same periodical[1], I intend to publish a separate series of papers on whorled phyllotaxis.

The aim of my researches will be a double one. In the first place they are a necessary complement of the general studies in phyllotaxis. As I pointed out beforehand[2] the wide-spread occurrence of whorls in flowers and in other parts of plants is not to be explained by any theory of phyllotaxis given as yet. In the second place we shall never get a right insight into the morphology of the flower, which is still the base of systematic botany, unless we get a clear idea of the relations between spiral and whorled arrangements in the flower. It is now nearly a century ago that von Martius enounced the opinion[3] that all floral whorls were in reality spirals. This view has since been shared by nearly all the leading morphologists[4]; and indeed the common case of a $^2/_5$ calyx is a very convincing argument.

Nevertheless nothing is known of the way in which spirals are transformed into whorls, and it is indeed very difficult to understand this phenomenon.

[1] I, Die Theorie, vol. X 1913, p. 153; II, Über verästelte Baumfarne etc., vol. XI, 1914, p. 95.

[2] l. c. 1913, p. 319.

[3] von Martius, Über die Architektonik der Blumen, Isis 1829, p. 335.

[4] cf. e. g. L. J. Čelakovsky, Über den phylogenetischen Entwickelungsgang der Blüthe und über den Ursprung der Blumenkrone II Sitz.-Ber. böhm. Ges. d. Wiss. Math. Nat. Cl. 1900 III; J. Velenovsky, Vergleichende Morphologie der Pflanzen, Prag 1905—1910, III p. 846.

The works of Schimper and Braun[1] contain a careful description of the facts which they observed in the transition of spiral to whorled phyllotaxis as seen in the adult condition: an explanation of the phenomena, however, was not tried.

All whorls are described by them in terms of spiral construction; the case of alternating whorls of four members is considered to be a $\frac{1}{4}$ phyllotaxis. Between the last member of a lower whorl (the cyclur) and the first member of a higher whorl (the cyclarch) the divergence is altered by the prosenthesis. Most authors on phyllotaxis have made the observation that the introduction of this notion of prosenthesis gave no explanation of the phenomena and that nothing was gained by it. Undoubtedly this is quite true, but when we carefully read the authors' descriptions, we come across some valuable elements. In the first place we admire their thorough observation, the detailed statement of facts. They were the first to see that whorls do not always alternate[2] but can also be put together in a more complex way, of which many instances are described. But perhaps their most valuable contribution is the distinction they make[3] between „untere Wirtel", low whorls, occurring in the vegetative regions of the plant, and „obere Wirtel", high whorls, in the inflorescences and in the flowers. According to the authors, the difference between them is, that pentamerous whorls in the vegetative regions are formed from a $^1/_5$ phyllotaxis, whereas the higher pentamerous whorls are $^2/_5$ spiral constructions.

It is quite probable that the conception of the low whorls as being derived from a $^1/_5$ spiral phyllotaxis will prove to be wrong; but that

[1] K. Fr. Schimper, Beschreibung des Symphytum Zeyheri und seiner zwei deutschen Verwandten der S. bulbosum Schimper und S. tuberosum Jacq., Geigers Magazin für Pharmacie Bd. 28, 1829, reimpressed in Heidelberg 1835 without the authors knowing; Al. Braun, Vergleichende Untersuchungen über die Ordnung der Schuppen an den Tannenzapfen etc., Nova Acta phys. med Ac. C. L. C. n. c. 15, 1831, p. 196; Al. Braun Dr. Carl Schimper's Vorträge über die Möglichkeit eines wissenschaftlichen Verständnisses der Blattstellung etc., Flora, 18, 1, 1835, p. 145, 161, 177.

[2] Symphytum, l. c. p. 82, Tannenzapfen, l. c. p. 360, S. 99.

[3] Tannenzapfen, p. 355, Vorträge, l. c. p. 164.

a hitherto unexplained difference between those two kinds of whorls exists, is in my opinion quite certainly the case, and a well-established theory of phyllotaxis should explain this remarkable difference.

Schimper and Braun did not try to explain the phenomena they described; Braun especially was inclined to think that any further step after the description of facts was impossible as these phenomena were the expression of ideas inherent to the living plant. Schimper was obviously more bent towards physiological conceptions and he promised to go „tiefer ins Physiologische" in his large work on phyllotaxis that was announced several times[1] but unfortunately has never been published.

Since that time, many investigators have studied the phenomena of phyllotaxis and many attempts to explain them on a more or less physiological base have been undertaken; but it is very remarkable that these attempts hardly bore on whorled phyllotaxis and chiefly endeavoured to make us understand the cause of the predominance of the numbers of the Fibonacci series.

Apart from a short paper of Goebel[2], in which whorls are derived from spirals in a phylogenetical way, no definite study of whorled phyllotaxis seems ever to have been undertaken.

This is the more surprising, as the whorled condition of phyllotaxis offers a very tempting problem, which morphologists as well as systematists often must have come across. The said problem is as follows. Since Hofmeister[3] in 1868 rejected the spiral-theory of Schimper and Braun, and expressed the opinion that leaves originate in the largest space between two lower leaves, this so-called law of Hofmeister has been the base of almost all theories on phyllotaxis. If this law holds true, the place of a leaf is determined by the position of two lower leaves, or if there are no lower leaves, by the boundaries of available space. Besides there may be various causes which act during the developmental stages of the

[1] Symphytum l. c. p. 119; Flora 18, 1, 1835, p. 39, ibid. p. 745.

[2] K. Goebel, Morphologische und biologische Bemerkungen, 21, Scheinwirtel, Flora 1912, 105, p. 71.

[3] W. Hofmeister, Allgemeine Morphologie der Gewächse, Leipzig 1868.

leaf, which may affect secondary displacements, the so-called metatopies. When we now consider e. g. a pentamerous whorled phyllotaxis with regular alternation of the whorls, this must be understood in this way that every leaf of a whorl is determined in its position by the two nearest leaves of the lower whorl; in using the notation of Church[1] this may be expressed by denoting the system as $5 + 5$.

A $^2/_5$ calyx on the contrary must be a cycle of a normal phyllotaxis of the Fibonacci series, and may be a $1 + 2$ system with 144^0 divergence.

Floral morphology has taught as further that most floral pentamerous whorls, which are not discernible from a $5 + 5$ system, must be derived from a $1+2$ system, or at least from a system of the normal series. Now it is clear that a given phyllotaxis can originate as $5+5$ or as $1+2$ but not as both at the same time. For a leaf the position of which has been determined by two lower leaves, cannot at the same time originate through the influence of two others; at the utmost the other leaves can afterwards cause a metatopy of the said leaf.

The changes required to make a $5+5$ system out of a $1+2$ system arevery considerable, and so the following two questions may be put:

Are all floral whorls really derived from spiral systems, or is it possible that there are two kinds of floral whorls, real whorls and altered spiral systems?

The second question is: by what processes are the metatopies induced, which change a spiral system into a whorled one? In respect to the first question, it may be remembered that Eichler has tried[2] to make a distinction between real floral whorls and false ones. He considered as characteristics of the false ones that the members originate in a spiral order and show differences in bulk or other peculiarities, connected with the same spiral order, and that this whorls are generally not alternating, but superposed. As true whorls on the contrary be considered those that are composed

[1] A. H. Church, On the relation of phyllotaxis to mechanical laws, London 1904.
[2] A. W. Eichler, Blüthendiagramme, Leipzig, 1875—78, part I, p. 8.

of similar members, arising and developing at the same time, and alternating regularly.

This distinction, however, was afterwards abandoned by Eichler: many whorls, which arise in spiral order, show afterwards no differences in any respect from real whorls, whereas other whorls, which arise simultaneously take afterwards the characteristics of the spiral system. Other whorls, which are both in their development and in their adult form undeniably spiral systems, notwithstanding alternate regularly. In all these respects Eichler found so many transitional stages that he was not able to draw a line between both forms, and three years later he was inclined to think that perhaps all floral whorls were contracted spirals[1].

This view, which has been shared, as mentioned above, by most morphologists, is still corroborated by the fact that leading authorities in systematic botany hold the opinion that the whorled condition in flowers is in general younger, and that the original flowers had only spiral arrangements of their parts.

In the above lines I hope to have made clear my double aim of consolidating the theory of phyllotaxis and of elucidating the floral morphology.

For the solution of the problems alluded to, it will be necessary to begin to study the whorled systems in the vegetative regions and the inflorescences.

For it is only in those regions that we can hope to meet clear conditions. In the flowers the whorls occur in so restricted numbers, and the succeeding whorls differ so much from each other, that the difficulties become too numerous.

In the vegetative regions the conditions are much more stable, a given system may be traced over a good deal of organs, and so there is much more chance to gather some knowledge of the acting causes.

As we shall see, in the vegetative region there are also different kinds of whorls. I will treat them in separate papers, and this first one will be devoted to a very clear and simple case of false whorls, that I have designed as growth whorls.

[1] ibid. II p. XIV.

2. Lilium Martagon. Among the several species of the genus *Lilium*, there are some which are mentioned in the literature as having whorled leaves. In Engler und Prantl[1], we find three of such species, viz. *L. Martagon*, *L. canadense* and *L. superbum*. Out of these three I have studied *L. Martagon L.* of which sufficient material grows in the Groningen Botanic Gardens[2]; as we shall see below, the two other species, as judged from the figures and tables in the literature[3] generally show the same conditions.

The shoots of *L. Martagon* are not throughout verticillate in all their parts. First the axis bears above the soil some singleplaced leaves; then come nearly always two whorls of large crowded leaves; above these there are again some smaller scattered leaves, which are in their turn succeeded by the still smaller bracts subtending the flowers.

The leaves of the two whorls, which are largest and most numerous, have obviously so much impressed the descriptive botanists, that very often the whole plant is said to have folia verticillata, in other cases however the scattered leaves above the whorls are also mentioned.

The number of whorls in the Groningen plants was constantly two; or in very weak and not-flowering shoots occasionally only one; in Curtis[4] we find that one to three whorls may occur. The number of leaves in a single whorl may differ considerably; according to Curtis there may be from four to twenty leaves in a whorl. Two succeeding whorls in most cases do not contain the same number of leaves; they are in no respect regular, alternating whorls. On nine stems I counted in the two whorls:

[1] Engler und Prantl, Die natürlichen Pflanzenfamilien II, 5, p. 60, 61; Leipzig 1888.

[2] Number 6844 of the Garden-Catalogue.

[3] For *L. canadense:* Curtis's Botanical Magazine, London XXI, 1805, tab. 800, XXII, 1805, t. 858, CI 1875, t. 6146, L. van Houtte, Flore des Serres. Gand, XI, 1856, t. 1174, XXI, 1875, t.2191, 2192. For *L. superbum* Curtis XXIV, 1806, t. 936, van Houtte X, 1855, t. 1014/5.

[4] l. c. C. 1874, text to t. 6126.

Shoot no.	Number of leaves		Shoot no.	Number of leaves	
	first whorl	second whorl		first whorl	second whorl
1	13	12	6	15	11
2	13	13	7	15	15
3	13	13	8	15	21
4	13	15	9	19	20
5	13	20	—	—	—

The same peculiar heteromery seems to occur in the two other Lilies, mentioned above; one of the figures in Curtis[1] shows a shoot of *L. canadense* with three successive whorls of 6, 3 and 4 leaves; and a specimen of *L. Superbum* in the Groningen herbarium[2] has two successive whorls of 10 and 8 leaves.

There are however also cases, viz. in *L. canadense*, in which no whorls occur at all, but all the leaves are scattered on the shoot; this appears from the description (foliis sparsis et verticillatis[3]) and from a figure[3].

From the foregoing it would seem, as if we had here a peculiar whorled phyllotaxis, which was not to be explained further in any way. A closer examination however, soon shows, that this whorled condition has arisen from a normal spiral phyllotaxis in a very simple and conceivable way, viz. by a very unequal growth of the parts of the stem between the leaves, some remaining undeveloped, whereas others attain a considerable length.

To give an adequate idea of the position of the leaves on a whole shoot of *L. martagon*, I have drawn fig. 1, which gives a representation in ½ natural size of the above shoot no 1, divided into six successive parts. In the middle of each part a dotted line marks an orthostichy of the stem (which was in reality a little twisted, in an irregular way, but which showed by the course of its fibres how the original orthostichy was to be followed).

[1] l. c. XXI, 1805, t. 800.
[2] from Biltmore Herbarium, 2651 b.
[3] Curtis l. c., C I, 1875, t. 6146.

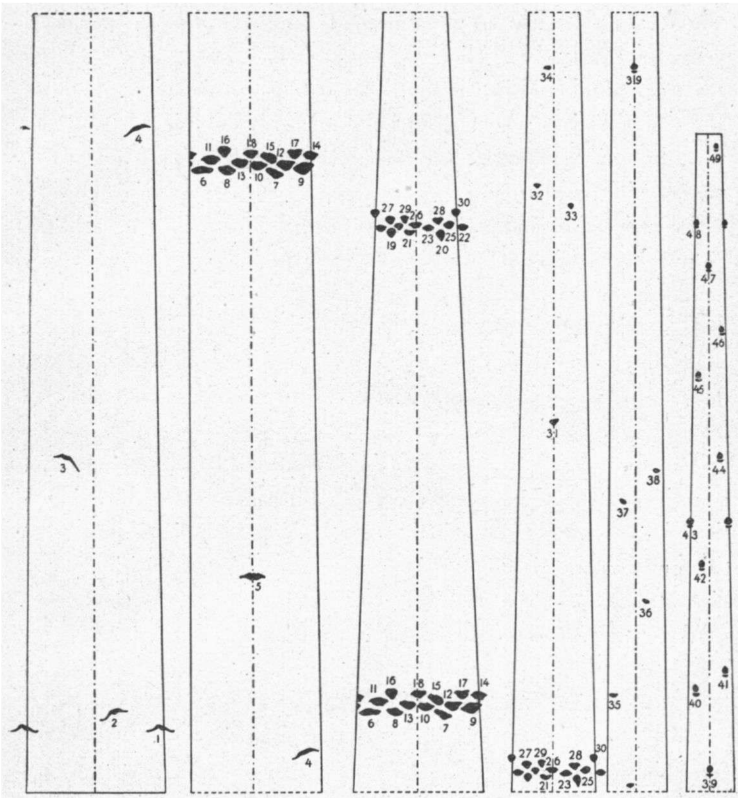

Fig. 1.

Lilium Martagon, surface of shoot with leaf-scars ½ nat. size. For explanation see text.

On both sides of this orthostichy the leaf-scars are drawn; the original drawing was in natural size. Those leaf-scars that lay on the opposite side of the stem, were represented twice, on the left and on the right; at last the straight lines at both sides of each part were drawn[1].

This figure will show that the five leaves, standing below the first

[1] As the shoot was not of the shape of a regular cone, but diminished in diameter especially above each of the whorls, these lines should properly have had another course.

whorl, are placed in a common right-winding spiral[1] with a divergence of nearly 135^0 ($1—5$ is nearly $360^0 + 180^0 = 540^0$). These scars are numbered in the figure according to this spiral. The leaf-scars of the first whorl appear not to form one single transverse row, but are placed at different levels. They even form clearly parastichies, and when we count these, there appear to be three in a right direction and five in a left one. These scars can therefore be numbered without any reference to the lower leaves, and when we do so, they form not only a phyllotaxis exactly of the same kind as leaves 1—5, but also their first member is the one (indicated in the figure as number 6), which stands just in the position it should have, if the whorl is the continuation of the phyllotaxis of the lower leaves.

The second whorl shows just in the same way three right-hand and five left-hand parastichies, and an independent numbering of these leaves shows that their first number is the one indicated as 19; this one has the right place in connection with the position of the highest member 18 of the preceding whorl.

Above the second whorl there are eight scars of scattered leaves. The first of them, 31 lies in the position it should have, as following from the position of the last number of the second whorl. The numbers 34—38 also lie in the expected situations, there is however a certain anomaly in the position of 32 and 33. It is true there are two leaf-scars on the orthostichies were 32 and 33 should be, but they are not in accordance with the expectation in so far, that 32 is without any doubt placed higher on the stem than 33. There is however no reason to change their numbers, for then the whole regular spiral would be disturbed. Especially when we consider that the bracts numbers 39—49 have such positions, that they form the direct continuation of the same normal spiral, we cannot avoid the conclusion that here is a certain metatopy, or that the internode between 32 and 33 has a "negative length" of 0.7 cm. From all this follows that the shoot under consideration has throughout one

[1] The direction of the spiral is taken as in most botanical works; right is ascending to the right as seen from the axis of the stem.

and the same normal Fibonacci phyllotaxis; this phyllotaxis appears undisturbed at the beginning (the first 5 leaves) and at the end (the bracts); in the middle part there are two kinds of deviations.

The first and for us the most important kind results from a very peculiar growth of the stem; the internodes above leave 5, above leave 18 and above leave 30, are stretched considerably, those between the leaves 6—18 and between 19—30 are hardly developed at all. As a result of this peculiar way of growing two agglomerations of leaves are formed, which are by no means true whorls, but which are sufficiently like whorls as to have always been described as such.

The second kind of deviation is the metatopy in longitudinal sense. A certain leaf-scar may grow up to a level, higher than that which would correspond to its order of sequence in the original phyllotaxis. This metatopy is only slightly represented here; if it had been more developed, the present investigation would have been much impeded. Differences of the same kind, but much smaller, are to be seen between the leaves of the two whorls; so 7 was placed a little below 6, 12 below 11, 20 below 19, 23 below 22.

The other shoots of the same species I examined, showed in every respect quite analogous phenomena. A second stem, number 6 of p. 190 with a quite regular left-hand spiral, will be sufficiently described by giving the lengths of the successive internodes.

Internode above leaf		1	2	3	4	5	6	7	8	9	10
Length in mm		13	48	6	61	53	27	82	37	88	3
Internode	11	12	13	14	15	16	17	18	19	20	21
Length	-1	0	2	-1	0	1	-1	2	-1	2	1
Internode	22	23	24	25	26	27	28	29	30	31	32
Length	0	3	127	2	1	-2	2	-1	1	2	-1
Internode	33	34	35	36	37	38	39	40	41	42	43
Length	2	2	110	46	9	32	31	4	34	12	117
Internode	44	45	40	47	48	49	50	51	52	53	54
Length	14	22	13	12	26	9	13	19	12	19	15

The whorls are formedby 10—24 and 25—35; the adjoining internodes are very long, just as the internode between the last sterile leaf and the first bract. All this is exactly as in the first specimen. The leaves 36—43 were sterile, 44—54 floriferous bracts.

A third specimen with again a just as regular right-handed spiral showed also similar conditions:

Internode above leaf		1	2	3	4	5	6	7	8	9	10
Length in mm		57	21	51	51	34	108	64	2	1	—1
Internode	11	12	13	14	15	16	17	18	19	20	21
Length	2	0	1	2	0	1	1	—1	3	125	1
Internode	22	23	24	25	26	27	28	29	30	31	32
Length	1	0	2	-1	2	1	0	1	0	1	2
Internode	33	34	35	36	37	38	39	40	41	42	43
Length	111	14	78	—4	25	8	—8	80	-14	151	16
Internode	44	45	46	47	48	49	50	51	52	53	54
Length	10	16	23	24	2	21	18	14	18	8	20

The first whorl is here 8—20, the second 21—33, the sterile leaves were 34—42, the bracts 43—54.

In the zone of the sterile scattered leaves there are here three „negative internodes", but apart from this, the most striking feature in the given figures is the close similarity to those of the two preceding stems. Considering the objects themselves, it is impossible not to recognize the regular spiral phyllotaxis, out of which the whorls are formed, the first leaf of the whorl lying just in the position prescribed by the lower leaves.

This kind of whorl, which simply arises by a peculiar kind of growth of the axis may be called growth whorls.

The idea, that whorls may arise by excessive growth of certain parts of the axis is by no means a new one. In the introduction I have already pointed out that Schimper and Braun took all whorls as contracted spirals and Delpino devoted several chapters of his „Teoria generale della fillotassi"[1] to the „sviluppi internodali regolari ritmici"[2] that gave rise to false whorls.

In all these cases, however, it was mere speculation without any conclusive evidence of the truth of the enounced opinions.

[1] Atti R. Univ. di Genova, Vol. 4, p. 2, 1883.

[2] l. c. p. 295—304.

They described the resulting whorls as quite regular; the partial growth of the axis should therefore have set in at a very early stage and the members of the future whorl should have been so little developed as to be still liable to be arranged in a regular whorl. It is very probable that in many plants this may be the case, but as yet it has nowhere been proved.

In the above considered case on the contrary, the growth of the axis is not altered before the primordia of the leaves are well developed; the arrangement of the numbers of the „whorl" remains the same, and the original phyllotaxis may easily be read even from the adult condition.

The distinction between growth and other whorls is not identical with the familiar distinction between true and false whorls. Growth whorls are a kind of false whorls, but it is by no means sure that the other whorls are all of the same kind and are all to be termed „true whorls".

3. Ferula thyrsiflora Sibth. et Sm. In this umbelliferous plant we shall come across a case of whorled phyllotaxis, that shows the greatest analogy to that of *Lilium Martagon* just described, in the higher cauline leaves and the lower bracts of the shoot.

The inflorescence of *Ferula* of course is a compound umbel; but this compound umbel is only part of a much larger mixed inflorescence, which might be called a compound raceme (panicle) of compound umbels, in which in main axis and first order of lateral axes the bracts are placed in more or less regular whorls.

Of these shoots[1] I examined 5 specimens. Of the main axis of one of these I made fig. 2, in the same way as in which fig. 1 of *Lilium* was drawn.

The first four leaves show clearly a left-hand ordinary spiral, the leaves 5—8 are already contracted into a kind of whorl; 9—11 however show the same left-hand spiral and are just placed in the spots required by that spiral. Leave 12—18 form again a conglomerate; 14 and 17 are placed somewhat higher than the rest. When we follow the „genetic" spiral, we come across some „negative"

[1] From no. 8971 of the Garden Catalogue.

internodes here; 14 is placed 9 mm higher than 15 and 17 10 mm higher than 18.

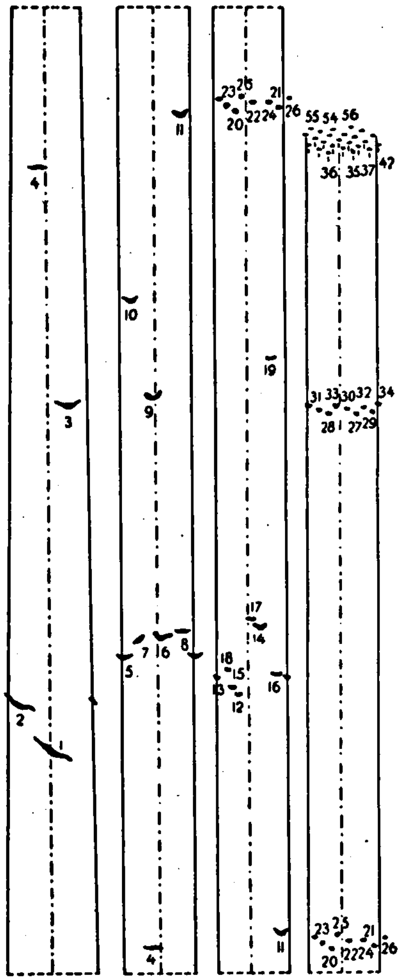

Fig. 2. Ferula thyrsiflora, surface of shoot with leaf-scars $^2/_3$ nat. size.

Leaf 19 stands solitary, on the place to be expected from the spiral; but 20—26 and 27—34 form very obvious whorls of the

same kind as those of *Lilium Martagon.* In these whorls there are clearly three left-hand parastichies to be seen; the numbers of leaves in them are too small to show the five right-hand parastichies, and the two right-hand are neither very clear.

But it is not be denied that even in those whorls a Fibonacci phyllotaxis with left-hand spiral is incorporated.

At the end of the stem, there was a terminal compound umbel, with 22 little umbels. These could all be numbered very regularly according to the same normal spiral. Only 13 of them, 35—47, arose from the axils of small bracts; the innermost 9 had no bracts at all. By the smalness of the top of the main axis it was not possible to render this part of the shoot in the figure at the same scale as the rest; the internode under the terminal umbel, which had a periphery of only about 6 mm was represented in the original figure with the same periphery of 14 mm as the lower parts; the position of the small umbels was partly plotted by construction. The bracts of the umbels are only indicated by small vertical lines.

This shoot shows us, that the whorls of bracts of *Ferula thyrsiflora* may arise in the same way as those of *Lilium Martagon* as growth whorls. The existence of a true normal Fibonacci spiral is clearly established by the regular arrangement of the umbels in the terminal compound umbel; the whorls themselves show three left-hand parastichies, so that there can be no doubt in that respect.

The four other shoots of the same plant I examined, showed generally similar conditions. Two of them had quite regular terminal compound umbels, as the one described, the position of the leaves and the bracts on the shoot was much of the same order as in the previous specimen, only still more regular in so far that they did not exhibit any „negative" internode of the stem. The fourth and the fifth shoot were somewhat less regularly built.

The terminal compound umbel of the fourth was composed of 17 rays, which were not quite regular in position and development. They might be numbered as 34—52 but the numbers 50 and 51 were absent; another anomaly was that 41 was only developed as a single flower, not as an umbel, while 49 which was placed behind 41 was an umbel again. The leaves and bracts on the shoot showed also more deviations from the regular position, as they had several „negative" internodes, one of them of 65 mm length. The fifth specimen was the most irregular; the „nega-

tive" internodes were numerous and large, and the terminal compound umbel, which was small and weak, was built of a mixture of single flowers and umbels of various size; it could not be numbered with any certainty. Here follows a survey of the lengths of the internodes of this shoot.

Internode above leaf	1	2	3	4	5	6	7	8	9
Length in mm:	32	46	70	−17	64	41	−33	109	−75
Internode	10	11	12	13	14	15	16	17.	18
Length	80	91	−8	45	−37	−8	45	−36	155
Internode	19	20	21	22	23	24	25	26	27
Length	1	0	133	-131	−2	134	−56	57	−3
Internode	28	29	30	31	32	33	34	35	36
Length	−2	7	−3	2	3	−3	7	−2	1

Although the metatopies were very considerable the divergence of the leaves and bracts was still quite normal. By the peculiar distribution of the growth of the stem, the position of the leaves becomes: 1—3 scattered, 4 and 5 near together, 6 and 8 near together, 7 and 10 at the same level, 9 and 11 near together, 13 and 16 at the same level and very near a second group composed of 12, 15 and 18; 14 and 17 together; 19, 20, 21, 23 and 24 together, 26 single, 22, 25 and 27—37 all in one conglomerate.

The terminal compound umbel followed close on 37 and was evidently much weakened by the development of 13 strong lateral axes just below it.

The foregoing observations lead us to the conclusion that in *Ferula thyrsiflora* the original phyllotaxis of the leaves of the shoot is a normal one of the Fibonacci series; in some cases more regular, in others less.

By a process of very unlike distributed growth of the different parts of the stem, the leaves are divided in single leaves, pairs of leaves and greater conglomerates; especially higher on, in the upper half of the shoot some true growth whorls are formed in this way. This process has nothing to do with the original phyllotaxis; whether this was a regular one or not the terminal umbel will show in unaltered fashion, as the elongation has not taken hold here.

This growth does not always take place in a certain internode or in some internodes; it is simply a transverse zone of the stem between the originally crowded leaves that stretches itself beyond measure.

The „negative" internodes of the stem may be so explained that this zone may be oblique and may pass over a higher and under a lower number of the original phyllotaxis. This is only a new proof for the thesis, already held by Braun[1] that the distinction between node and internode is only valuable in the case of the simple terms of the phyllotaxis series, but that in the higher terms, as soon as several leaves are inserted on the stem side by side, the distinction looses its significance.

4. The inflorescence of Primula. It is a well known phenomenon in several species of the genus *Primula*, that the inflorescence, instead of forming a single umbel, has two, three or more distinct zones each with numerous flowers. These zones are sometimes called superposed umbels, in other cases they are designed in the literature as whorls.

A simple investigation was sufficient to show that in these inflorescences we have without any doubt another case of the same growth whorls as described of *Lilium* and *Ferula*.

A species I examined was *Primula Bulleyana* Forrest[2], from the Groningen Botanical Gardens. Just as in the former cases, the numbers of the flowers in the succeeding whorls did not show any correlation; so in ten inflorescences I counted:

Inflorescence	Numbers of flowers in the						
	1st	2nd	3rd	4th	5th	6th	7th whorl
1	1	12	14	12	8	8	5
2	10	9					
3	11	11	8	14			
4	5	12					
5	13	15	15	14	13		
6	7	14	8	12			
7	11	15	14	14	11	10	9
8	8	11	10	14	9	7	
9	8	15	14	10	14		
10	8	11	13	14	8		

[1] Tannenzapfen, l. c. p. 345.

[2] No. 11493 of the Catalogue.

In the different whorls the insertions of the flowerstalks are not at the same level; in fig. 3 a representation is given of the position of the flowers in the first inflorescence from the above table[1].

In every whorl of the living object five left-hand parastichies and eight or three right-hand ones were very conspicuous; in the drawing they are also to be seen. Every whorl could therefore be numbered quite independently; in the figure the lowest and the highest numbers are indicated. In all the whorls the lowest number was just placed at a normal divergence from the highest member of the foregoing whorl. It is therefore clear, that the bracts subtending the flowers have been formed in a normal phyllotaxis, and that the appearence of superposed umbels has arisen from the some partial elongation of the main axis which was the cause of the growth whorls described above.

Other *P.*-species show similar conditions, such as *P. imperialis* Jungh., *P. Kewensis* and *P. obconica*. In *P. sinensis* two inflorescences with 4 and 5 growth whorls showed the following numbers of flowers in the whorls: 5, 6, 7 and 4 in the one and 3, 6, 6, 4 and 6 in the other specimen. The parastichies of the insertions of the flowerstalks were not clear, owing to the small number of stalks in a single whorl; the character of growth whorls was however quite evident from the variability of the number of flowers in the whorls.

5. *Polygonatum verticillatum.* Aug. 1921 I collected on Mount Pilatus in Switzerland a number of shoots of *Polygonatum verticillatum*. In every shoot a scar of a stem-clasping bract was to be seen at the base; higher up there were from one to seven whorls of ordinary leaves. None of the shoots was flowering. The whorls themselves presented in some respects a close analogy to those of the three cases mentioned above; in other respects, however, there were differences.

The table below gives the number of leaves in the successive whorls of the collected shoots. In some of the specimens the successive whorls are quite unlike in number of leaves, e. g. number 17,

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[1] In each whorl the differences in height of the insertion are exaggerated; and since no attention has been paid to the diminishing diameter of the tapering main axis, the lateral distance of the members of the higher whorls is drawn too large.

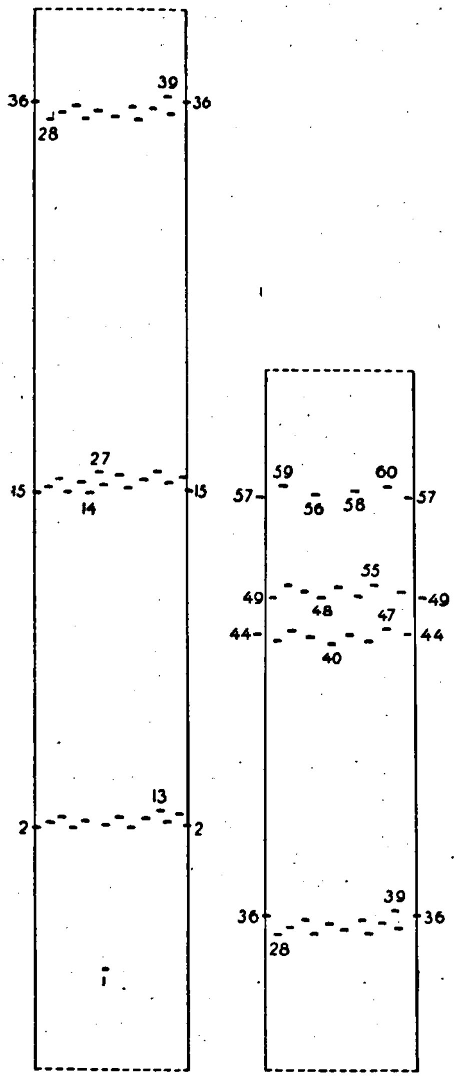

Fig. 3. Primula Bulleyana, surface of flowershaft with scars of bracts $^{2}/_{3}$ nat. size.

Polygonatum verticillatum			
Shoot	Number of leaves in the successive whorls	Shoot	Number of leaves in the successive whorls
1	3, 6	12	3, 6
2	4, 4, 4, 4, 4, 8	13	3, 6
3	6	14	3, 6
4	3, 7	15	8
5	3, 1, 9	16	4, 7
6	4, 2, 6	17	3, 1, 2, 3, 7
7	6	18	4, 4, 8
8	3, 5	19	4, 2, 3, 6
9	4, 4, 4, 4, 4, 4, 4	20	4, 4, 4, 4
10	6	21	3, 3, 7
11	3, 6	22	5, 3, 8

in others as 9 and 20 all whorls have the same number of leaves.

On closer examination this curious contrast was readily explained; the shoots in question had without exception originally a whorled phyllotaxis with trimerous (numbers 1, 3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 19, 21) or tetramerous whorls (numbers 2, 9, 18, 20, 22). The growth of the stem had however not taken place in the usual way, so as to separate the successive whorls from eachother, but in many cases one or two leaves of a certain whorl remained attached to the lower or the higher whorl. The mutual positions of the leaves in the so resulting agglomerates were quite unaltered, so the real status was easily recognised. At the top of most shoots two whorls were placed together; only in a minority there was one whorl, while in others the terminal agglomerate contained not strictly two whorls, but one or two leaves more or less.

The numbers 1, 11, 12, 13, 14 had three trimerous whorls, the highest two of which were combined in a terminal agglomerate; the numbers 3, 7 and 10 had only such an terminal agglomerate.

Of the tetramerous shoots number 2, 9, 18 and 20 need no explanation, they were perfectly regular tetramerous, with two combined whorls or a single one at the top.

The other shoots were all more or less different from the normal scheme, they showed the following conditions.

Number 4 had one trimerous whorl, an agglomerate of two regular alternating trimerous whorls and in the centre of this agglomerate one odd leaf.

Number 5 had one regular trimerous whorl, then one single leaf, placed between the orthostichies of two leaves of the lower whorl, and then a terminal agglomerate, consisting of two leaves which formed a complete trimerous whorl with the lower single leaf, two regular alternating trimerous whorls and lastly one single leaf in the middle, in the position of one leaf of an alternating trimerous whorl.

Number 8 had one normal trimerous whorl, and a terminal agglomerate of one regular trimerous whorl and one of two leaves; the last standing in the position of two of the leaves ot a trimerous whorl.

Number 15 with only a terminal agglomerate of 8 leaves was by no means tetramerous, but had two regular trimerous whorls and a third whorl of two leaves, standing in the position of two of the leaves of a trimerous whorl.

Number 16 was also trimerous, the lowest whorl consisted of a regular trimerous whorl with the addition of one leaf, placed somewhat higher between two of the three; the terminal agglomerate at first contained two leaves, forming a second trimerous whorl with the odd leaf below, and further on a third trimerous whorl and two leaves of a fourth one.

Number 17 possessed one basal trimerous whorl, a second which was divided into one single leaf and two placed together higher on, then a third regular whorl and a terminal agglomerate of 3+3+1 leaf.

Number 19 had a lowest whorl of 3+1, then two leaves forming a regular alternating whorl with the lower odd leaf; the rest was regular trimerous.

Number 21 was quite regular trimerous, except a seventh odd leaf in the centre of the terminal agglomerate.

Number 22 was just as regular tetramerous, only one leaf of the second whorl was displaced to the first whorl.

From the foregoing our conclusion must be that *P. verticillatum* has originally a whorled phyllotaxis with crowded whorls; that when elongation begins it takes hold in many cases of the internodes between the whorls, and a regular whorled condition is arrived at, in other cases the elongated parts of the stem are other irregular oblique zones, and the result is that the numbers of the whorls seem to te changed.

The term growth whorl may quite well be applied to this case; the peculiar distribution of growth is here quite the same as in *Lilium Martagon*, it is only applied to another preexisting arrangement of leaves.

6. *Elodea.* The common Waterthyme, *Elodea canadensis* is well known for having trimerous whorls of leaves; one would therefore think it out of place to treat this plant here.

There are however in *Elodea* sometimes slight deviations from the normal whorled condition, just in the same way as those described in *Polygonatum.*

Eichler describes in his „Blüthendiagramme"[1] that the flower arises in the axil of a leaf of a tetramerous whorl, which is followed on the main axis by a dimerous one; the mutual position of the leaves is so (cf. fig. 40 B), that the lower tetramerous whorl consists of a trimerous one with one supernumerary leaf, taken from the next higher whorl, of which remain only two leaves.

In not-flowering vegetative axes the same phenomenon will sometimes occur without any flower or axillary shoot; a growth whorl of 3+1 leaf is followed by another of 2 leaves.

More clearly the some phenomenon is showed by *E. densa* Casp. of which I studied some shoots out of our botanical garden[2]. Here the axillary buds never occur in the axil of a leaf of a normal whorl, but where a bud is present the whorl in which it occurs is always united to the whorl below. In trimerous shoots the whorl gets in this way six members, in tetramerous shoots eight. In numerous cases slight irregularities are added; instead of a double whorl of six leaves we find e. g. one of 3+2 leaves, while the next one counts 1+3; or instead of three tetramerous whorls there are developed two of 4+3 and 1+4 leaves. In these cases the original alternation of the whorls is always retained; the first growth whorl consists of one regular tetramerous whorl and three leaves placed clearly over three of the four spaces; the next growth whorl then contains one lower member, falling over the fourth space, and an alternating regular tetramerous whorl.

On a much smaller scale we have therefore just the same phenomenon as in Polygonatum; we may say that Elodea has ordinary whorled leaves, with a slight tendency to the formation of growth whorls.

[1] Eichler, l. c., I p. 92.

[2] No. 11057 of the Catalogue.

7. *Discussion.* The here described cases have all this in common that a stem with originally crowded leaves is divided by an unequal growth into bare and into leafbearing parts.

These leafbearing parts assume in this way a certain resemblance with whorls, and in some cases they have been described in the literature as whorls.

It is clear that these formations, to which we have given the name growth whorls are to be considered as a kind of false whorls, and that nothing is yet said about the nature of true whorls nor of other false whorls, as they occur in flowers. But it seems to me that before the problem of whorl-formation in the vegetable kingdom can be properly taken in hand, it will be useful to seclude from the rest of the whorls the formations which have been described here and which form clearly a kind of secondary transformations, originating only late in the development of the shoot. As to the way in which this distribution of growth is determined I can give no indications as yet; we may perhaps make only the following remarks.

In the Umbelliferous plants the formation of the umbels depends upon a stunted growth of the internodes between the rays; the growth whorls of the leafy stem of *Ferula* may therefore have arisen from a mixture of the factors that cause the ordinary growth of the internodes of the stem and of those that cause the stunted growth in the umbels; it would therefore be a partial spreading of a factor, that ordinarily only acts in the inflorescence, to the stem.

In *Primula* we have in the same way the contrast between the vigourous growth in the majority of the species of the basal part of the flowershaft and the stunted growth in the terminal umbel; in most species these two processes are quite separated and the result is a single umbel. In others they are intermixed as we have seen, so that they form growth whorls; a third category is formed by those species as *P. acaulis*, where there is no flowershaft at all („scapus nullus") but only a sessile umbel between the leaves.

It is clear however, that these considerations give not yet the explanation of the phenomena, and in the other cases not even this partial comment can be given.

About the distribution of growth whorls among plants nothing is to be said with certainty as yet. But it is not improbable that growth whorls will prove also to be present in several other plants.

A similar case is described by Drude for *Styphelia verticillata*[1], the whorls of it „stellen in Wirklichkeit nur dicht gedrängte Spiralen mit zwischenstehenden, lang-blattlosen Stengelgliedern vor", so that the „Blütenähren zahlreich aus mehreren, wie Stockwerke übereinander gebauten Scheinquirlachseln gleichzeitig hervorbrechen."

8. *Summary.* A bud with a crowded number of foliar primordia, may develop into a shoot with more or less defined whorls of leaves by the simple growth of certain zones of the stem, while other zones remain short. This kind of whorl is heteromerous and the leaves in a single whorl are not equidistant, and not placed all at the same level, but their insertions show more or less clearly the parastichies of the original phyllotaxis.

The above described whorls are termed growth whorls and regularly occur in *Lilium Martagon*, *Ferula thyrsiflora*, in several *Primula spp.*, in *Polygonatum verticillatum* and probably in many other plants.

Groningen, Botanical Laboratory
of the State University, Dec. 1921.

[1] Engler u. Prantl, Die natürlichen Pflanzenfamilien IV, 1, 68.